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RP
Heptane

January 27, 1928

JEFFREY PINE AND ITS RELATIONS TO WESTERN YELLOW PINE

by

N. C. Tihomiroff

California Forest Experiment Station

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The taxonomic position of Pinus jeffreyi Murray[2] (P. jeffreyi Balfour,[14] P. jeffreyi "Oregon Committee"[25]) and its relation to P. ponderosa Lawson have long been subject to differences of opinion on the part of botanists. Recent experimental work connected with the tapping of these two trees for oleoresin, conducted by the writer for the Forest Service, afforded an opportunity to obtain some interesting material bearing on the status of Jeffrey pine.

Jeffrey pine was discovered in 1852 by John Jeffrey and was named by Professor Murray, the description being published by Professor Balfour in the "Report of the Oregon Committee". Since that time it has been variously described as a distinct species and as a variety of western yellow pine. Jepson[15] designates it P. ponderosa var. Jeffreyi Vasey. Britton[7] describes it under the same name, though he remarks that this pine is "quite distinct (from P. ponderosa) and may perhaps be deserving of specific rank". Again Howell,[13] Sudworth,[26] and Abrams[2] consider it a distinct species.

One of the earliest and most observant students of

Jeffrey pine was Professor J. G. Lemmon[18]. In a careful study of Jeffrey pine over a period of twenty years, he collected many important facts regarding this species, its range, occurrence and varieties, and gives in his publications many useful and valid characteristics of this species as well as of western yellow pine.

Lemmon arrived at the conclusion that Jeffrey pine, "which has all along been called a variety of ponderosa", should be accorded "rank of a distinct species". Besides the typical Jeffrey pine (of Jeffrey's discovery) Lemmon detected three "marked forms", namely: (1) ambigua, (2) peninsularis, and (3) deflexa.

His variety "ambigua", given as occurring in Montana, apparently was based only on a form described by Sargent as occurring in that state and referred by Sargent to western yellow pine. So far as is known to the writer there is no indication in later literature that Jeffrey pine occurs in Montana. Specimens of foliage and cones recently sent to the writer from the locality mentioned by Lemmon seem unquestionably to be western yellow pine. There is, therefore, much doubt whether Lemmon's variety "ambigua" can be referred at all to Jeffrey pine.

The variety "peninsularis" was found by Lemmon "on the peninsula of Lower California on the San Raphael Mountains at an elevation" (quite unusual for this species in such a low latitude) "of about four thousand feet. It forms an

extensive forest upon loose debris of white granite". According to Lemmon, the bark of this variety is grayish or darker, deeply furrowed; cones remarkably abundant, 6-8 inches long, scales large with strong umbos and thick, firmly deflexed prickles.

The variety "deflexa" (P. deflexa Torrey)[x] is common in the higher Sierra in California. The bark is reddish brown, thick and coarsely checked by wavy lines; leaves glaucous.

Among the four varieties of P. ponderosa mentioned by Lemmon,[18] the variety "nigricans" is very interesting in connection with the present study. Lemmon describes it as a tree of medium size (120-150 feet) with the bark dark brown or almost black, hard, rather coarsely checked.[xx] He says, "This form is generally found in company with the larger typical whitish-barked trees. It is particularly prevalent in small valleys and along the edges of forests in the Sierra.

"This form has been confounded with forms of Jeffrey pine, but may always be distinguished by its lighter colored bark, its smaller and narrower cones, its leaves apple-green, never glaucous; also by its terebinthinous, not aromatic odors."

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x - Jeffrey pine was discovered by Parry three years before Jeffrey's discovery, but published later (in 1858) by Torrey as P. deflexa - see Lemmon, first report p. 100.

xx- Typical yellow pine has light yellow soft bark, divided into large plates.

The study made by the Forest Service, above mentioned, was carried out by the writer in the summer of 1927, chiefly in the Lassen National Forest, about thirty miles northeast of Lassen Peak.

The experimental area was located on a gentle southerly exposure, the elevation ranging from 5700 to 6100 feet. The stand was composed of both Jeffrey and western yellow pines with predominance of the former. Scattered junipers occur here and there in the stand. On the more rocky places specimens of Cercocarpus ledifolius appear. The lower part of the area bordered on an extensive open flat, the fringes of which were covered with Artemisia tridentata. Herbaceous vegetation was represented by species of Lupinus, Wyethia, Chrysothamnus, and Gramineae. These plants were rather scattered, never covering the ground completely. The soil is of volcanic origin, developed upon quaternary basaltic lava, well decomposed and relatively fresh.[x] The physical conditions of this area seem to be in accordance with Lemmon's suggestion that typical Jeffrey pine occurs on "those slopes which were first left bare by the withdrawal of the ice at the close of the Glacial Epoch".

Typical forms of both Jeffrey and western yellow pine were present and little difficulty was experienced in distinguishing between them. The former has characteristically dark brown to cinnamon-red bark, irregularly furrowed,

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x - The more complete discussions on physical conditions of the place will be found in the writer's official report of experimental heptane production.

the cones being 5-6" long, shaped like an "old fashioned straw bee-hive".[17] The latter has, when mature, dull, light yellowish bark with large, squarish flat plates, and small cones 2-3" in length.

Cones of typical trees of these two species exhibit quite pronounced differences, not only in size, but in scale arrangement and shape of prickles. The scales of Jeffrey pine are more numerous, projecting almost horizontally from the axis of the cone, and are armed with long, deflexed prickles (Plate I, fig. 1-4). The cone scales of western yellow pine are fewer in number, more irregularly spreading from the cone axis, with short, erect prickles.

Lamb,[25] based upon "observations in the field and in the large herbaria of the United States" considers the difference in shape of cone scale as a very consistent one for distinction between the two species. According to this author, "the cones of yellow pine have scales with short, broad prickles" (which are erect, as his attached drawing shows). The cones of Jeffrey pine have slender down-curved prickles.

Plate 1 shows variations in the cone scale shape as observed by the writer in the field. It is evident that the use of this character as a basis for distinction in the case of non-typical forms would lead to confusion. Lemmon (op. cit.) in his diagnoses always describes the shape of western yellow pine prickles as being erect or incurved. As

a rule, on the present experimental area, Jeffrey pine has prickles either deflexed or rarely hooked backward. In only one case were cones of this species found, near Westwood Junction, armed with erect short prickles (Plate I, fig, 7 & 8). This may be assignable to individual variation.

There are indications[9] of consistent differences between the buds of these two species of "broken cone pines".[x 18] The buds of Jeffrey pine are non-resinous while those of yellow pine are covered with numerous resin droplets. This character has been checked for many specimens and has proved to be constant, at least for the places where these pines have been studied in California. It is noted, however, that in the specimens of western yellow pine foliage recently received from Montana, as above referred to, the buds are not resinous (Plate I, fig. 17 & 18).

The bark of Jeffrey pine varies much in its texture and color. Sometimes it is lighter than that of non-typical yellow pine (compare var. nigricans, Lem.). The main differences in the bark of the two species, based on examination of hundreds of trees in the field, appear to be as follows: in Jeffrey pine, the color of newly exposed inner bark scales varies from grayish to brownish tan; in

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x - The fracturing of cone base is common for western yellow pine as well as for Jeffrey pine, undeveloped basal scales persisting on the limb.

xx - Compare Jepson[16] page 40 and Lemmon[18] pages 97 and 197.

the case of western yellow pine these scales are consistently light yellow in color, appearing as if powdered with sulphur.[xx] This distinction is nearly constant for both typical and non-typical trees. It is of interest to note that the scolytid beetle, Dendroctonus jeffreyi Hopkins,[11] apparently makes a sharp distinction between Jeffrey pine and western yellow pine. This Dendroctonus (and no others) frequently attacks Jeffrey pine and it very infrequently, if ever, attacks western yellow pine. The writer has never found it attacking the latter, although Hopkins[2] states that it sometimes does so.

Differences between Jeffrey pine and western yellow pine are very clearly distinguishable in the juvenile stage. When young trees are considered, intermediate forms are no longer apparent. Young western yellow pines are distinguished by buds which are always resinous, by the young brownish-green branchlets "shining as if varnished" (Lemmon, loc. cit.). The bark of the upper part of the stem and smaller branches is grayish, marked by rather coarse yellow-brown longitudinal fissures. The foliage is bright green in color. Young Jeffrey pines have non-resinous buds (somewhat different in shape, see Plate I, fig. 17 & 18), the branchlets are pruinose and the bark of the upper stem is smooth and light gray in color with a somewhat purplish hue, resembling the bark of young firs.

xx - Compare Jepson[16] page 40 and Lemmon[18] pages 97 and 197.

The leaves are bluish green, contrasting very distinctly with the yellowish green ones of the western yellow pine.

According to G. R. Shaw[12] the pruinose branchlets of Jeffrey pine are associated rather with a dry environment than with a species. This statement does not seem to be in accordance with present field observations, since the pronounced differences in the branchlets were found between Jeffreyi and ponderosa growing side by side under the same environmental conditions. It is of particular interest to note that the writer has found the bark of young Jeffrey pines, before it becomes fissured with age, to be marked uniformly by numerous resin-filled pustules, like the bark of fir. These pustules have never been found by the writer on the bark of western yellow pines.

Besides the morphological differences between P. jeffreyi and P. ponderosa, a marked distinction is found in the leaf anatomy of these species. As shown by Plate II, P. ponderosa needles have a single row of thin-walled cells between the epidermis and the cortical heavy-walled sclerenchyma cells; P. jeffreyi needles have no thin-walled cells in the cortical region, strengthening tissue being just beneath the epidermis. It should be noted that the cells above called thin-walled are hardly so in the sense in which parenchymatous structures such as internal mesophyl may be thin-walled; but they are strikingly thinner walled than the epidermal and strenghtening cells adjacent to them.

Coulter and Rose[8] found no difficulty in distinguishing this thin-walled layer in the case of the pines under consideration and they suggested that this character is of considerable importance. This was verified by Lamb[25] and has been checked for a large number of specimens by the writer. Various writers have indicated a significant difference in the number of cotyledons of Jeffrey pine and western yellow pine[26]. The writer has failed to find any significant difference in respect to this character, the number of cotyledons for both pines as examined by him varying usually from 8 to 12, in most cases being ten.

It should be expected that the geological record would throw considerable light on the problem of taxonomic relation, but the hope is in this case vain. Professor Lemmon stated that Jeffrey pine was not only an older form than ponderosa but should be considered the ancestor of this comparatively younger species. What his basis was for such a statement can only be conjectured. The writer understands from paleobotanists that, while fossil three-leaved pine material occurs as far back as possibly the Jurassic, there is none of it which has been definitely assigned to either of the species under consideration. These species, in short, may be said to have practically no fossil record, at the present time.

It is not understood, however, that paleobotanists have ever attempted the application to this purpose of the differences in leaf anatomy first called to attention by Coulter[8]. It is suggested that there may be possibilities through redetermination by its aid of fossil material, of carrying one or both of these species back into the record of that geological past in which they must have been represented.

Non-typical forms (past the juvenile stage) displayed such variations in appearance that frequently very close inspection was necessary to determine definitely whether ponderosa or Jeffreyi was represented. Careful study confirmed the conclusion of C. S. Smith[25] and others that few of the intermediate forms are referable to P. jeffreyi, while those of P. ponderosa were found in abundance. In fact, when in accordance with the plan for the experiment previously mentioned, an attempt was made to establish five groups of trees (and to select five specimens of each) showing five morphological gradations between typical Jeffreyi and typical ponderosa, abundant non-typical yellow pines were found without difficulty, but only four such specimens of Jeffrey pine (out of hundreds) could be selected. Three of these individuals had been selected on account of their rather light reddish bark and some variations in the shape of prickles, as shown in Plate II, fig. 5 & 6 (var. deflexa?), the last one

because its soft bark, with yellowish newly exposed flakes and the prickles being characteristic of Jeffrey pine (Plate I, fig. 4). All these pines were found to be heptane producing trees, and were, therefore, classified as Jeffrey pine forms, on the strength of the apparent determinative significance of this character, which is discussed below in connection with the chemical aspects of the study.

The distinction between Jeffrey pine and non-typical forms of western yellow pine by means of morphological characters is not easy. Nevertheless, experience indicates that by close study, one can almost always find some constant morphological characteristics present. If the cones are not typical, the appearance of the outer bark or the color of the newly exposed bark layers may help in identification. Only one specimen among many examined might have been taken for Jeffreyi both on the basis of the size of the cones (5") and the rather hard dark bark with inner flakes not of the prominent sulphur-yellow color characteristic of ponderosa, but was clearly indicated to be ponderosa by the terebinthinous odor of the oleoresin (obtained by boring with a knife through the bark to the cambium).

The validity of this odor as a diagnostic character between these two forms, especially as a last resort

when morphological evidence is inconclusive rests upon differences in the chemical composition of their oleoresins which appear to be completely constant, at least in the area studied by the writer. The chemical peculiarities of Jeffrey pine, indeed, are so important that they should be given special consideration.

The oleoresin formed in the wood of P. jeffreyi contains an aliphatic hydrocarbon, normal heptane (C_7H_{16}), and none whatever of the mixture of terpenes ($C_{10}H_{16}$) usually found in pines. Only two plant species besides Jeffrey pine are thus far known to contain heptane - P. sabiniana[21], also a California pine, and Pittosporum resiniferum[3], a tree of the Philippines.

The occurrence of a hydrocarbon of the methane series in the oleoresins of California pines was first reported by Professor Wenzell[27] in 1872, to the great surprise of chemists, and caused an extensive discussion[23] until as late as 1899. Gildemeister and Hoffmann[11] suggested that probably Wenzell's abietine (heptane) was simply a petroleum fraction. Until 1904, the botanical source of abietine was an open question[28].

In 1913, oleoresin samples of Jeffrey pine were analyzed by Schorger[21]. Two years later Adams[1] tested a sample of oil obtained by steam distillation of wood from an

authoritatively identified Jeffrey pine. Both authors found that the bulk of the oil consisted of n-heptane. The occurrence of heptane in Jeffrey pine is, therefore, a well established fact.

The composition of the oleoresin of Jeffrey pine appears to be as follows: the volatile part consists of n-heptane (about 95%) and small amounts of n-decylic aldehyde, linalool and methylchavicol.[20] The non-volatile part (rosin) consists of 12.5% resene, the balance being mainly abietic acid.

It is of interest to note that the oil from the twigs and needles of Pinus sabiniana consists of terpenes[14] and that the fruits (nuts) of Pittosporum contain both a dihydroterpene ($C_{10}H_{18}$) and n-heptane.

In the case of Jeffrey pine, it has been found both by the writer and by Dr. Eloise Gerry of the Forest Products Laboratory of the U. S. Forest Service, that the bark contains resin ducts as well as the resin pockets which have been referred to, and both of which appear to have a direct relation to the oil also found in the bark. In view of the fact that the oil from the bark of Jeffrey pine had not previously been examined, the writer distilled samples of the bark of young trees. Specimens were selected which exhibited typical morphological characteristics of Pinus jeffreyi and contained heptane in the wood. Care was exercised to prevent any woody parts being distilled, in order

to avoid confusion with the wood oleoresin as happened in the case of the twig distillation of Digger pine as reported by Schorger.[21]

A small sample (30 g.) of oil obtained by steam distillation of the twig and upper stem bark was examined. The fractions were separated at each 10° decade point after boiling commenced, which was premised on the boiling point of α-pinene at 156° C. and that of β-pinene at 163° C., so as to separate out these two possible constituents. The following table shows the constants of this oil; Schorger's[21] data for western yellow pine and Digger pine are also given for comparison:

Constants	Jeffrey pine	Western yellow pine	Digger pine
Specific gravity at 15° C.	0.8659	0.8718 - 0.8849	0.8517-0.8566
Optical rotation at 20° C. in a 100 mm. tube	-25.86	-15.73 - 19.59	-20.93-38.36
Index of refraction	1.4715	1.4789 -1.4815	1.4670-1.4708

The oil was submitted to fractional distillation with the following results:

Number of fractions	Temperature centigrade	Distillate observed %	Distillate cumulative%	Index of refraction 20°C.
1	150 - 160 (mainly 155)	32	32	1.4630
2	160 - 170	40	72	1.4685
3	170 - 180	6	78	1.4710
4	180 - 220	11	89	1.4743
residue		9		1.4880
losses 2%				

On the suggestion of Professor W. H. Dore of the Laboratory of Agricultural Chemistry, University of California, where, by his courtesy, the distillation was carried out, each fraction was tested by means of Schiff's reagent for the possible presence of furfural. The aqueous extract gave a deep violet color instead of the rose color usual for furfural. The violet color was especially strong in fraction 3. This reaction appears to be thus far unknown.

Owing to the small amount of oil, no more definite information could be obtained. Nevertheless, this rather incomplete test seems to be of a considerable importance. It shows that the composition of Jeffrey pine bark oil is entirely different from that of oil obtained from wood of this species. As the oil started to boil at 155° C. it is safe to conclude that n-heptane (boiling point 98° C.) is absent. Judging from the boiling points and physical constants of Jeffrey pine bark oil, it appears that this oil consists, as usual for the genus Pinus, of terpenes with the possible presence of esters. It is of interest to note that more than 70% of the oil distilled between 155° and 165°. It appears, therefore, that probably pinene (α and β) is the chief constituent of this oil. It would be highly desirable to collect a greater amount of this oil for further investigation. From the field experience it appears that the oil present in needles and cones of Jeffrey pine also contains no heptane, but consists of terpenes.

The chemical composition of the oleoresin of western yellow pine has been determined by Schorger (loc. cit. p. 754). The volatile oil contains 5% a-pinene, 60% B-pinene, 20% limonene, and 10% of sesquiterpene (cadinene). The rosin contains about 90% abietic acid.

The difference, therefore, in the composition of the oils of the two species under consideration is beyond doubt. It remains to be seen whether these chemical differences throw any light upon the taxonomic relations between ponderosa and Jeffreyi. It must be emphasised at the beginning that the conclusiveness of the presence of heptane or terpenes, respectively, with respect to the identity of the specimen as P. jeffreyi or P. ponderosa says nothing respecting the rank of either of these forms in the taxonomic scheme or, in other words, whether the former is entitled to that specific name or should have a varietal cognomen added to it. Lemmon in his descriptions always mentions differences in odor between the two species (due to the different chemical composition). Mueller in his Eucalyptographia[19], describing Eucalyptus piperida, states that the chemical peculiarities of the bark and wood may possibly be used to distinguish this species from E. obliqua. Some authorities consider differences in chemical composition insufficient grounds for the taxonomic separation of forms. In 1914 Lamb[25] pointed out that "such methods cannot contribute greatly to the distinction of species." Twelve years before this statement was made,

an excellent work on Australian Eucalypts[4] appeared in print, whose authors "adopted a system of classification based not on morphological characters of dried material alone, but on (1) a field knowledge of the trees; (2) the nature and character of their bark and their timber; (3) the morphology of their fruits, leaves, buds, etc.; and (4) the chemical properties and physical characters of the oils and the utilization of any other evidence such as hystology". For any given species they found a well determined constancy in the chemical composition of the oil. In other works[5,6] Baker and Smith point out that "a remarkable constancy is found in the chemical constituents of the oil of any particular species wherever grown" and that the constancy in the chemical composition of the same species is of great value in the distinction between the several species. These authors concluded that the chemical composition may safely be used for distinction between species, especially when the morphological characteristics are not clear enough. Finnemore[10] in his recent book says that "this method may be of interest in the study of other volatile oils but it must be used with caution" outside of Australia as that continent represents a flora which has been established a relatively long time. Schorger[22] found that there is a chemical constancy for P. ponderosa var. Scopulorum from different places. Again, typical western yellow pine has the same chemical constancy either in Washington or in California.

One of the most uncompromising views against the validity of chemical composition as a basis of taxonomic diagnosis, recently expressed verbally to the writer by a very eminent American botanist, rests the case against it upon the ease with which artifically produced varieties of plants can be changed in their chemical characters. Apparently, however, this might be admitted without its proving that chemical composition was thus unstable under natural processes. That changes in chemical composition have occurred in the evolutionary process seems inevitable in view of differences in this respect between genera, and even species, of undoubted common origin. But the causes of such changes, the extent to which they accompany smaller steps in the evolutionary process, and thus the limits within which chemical differences may be diagnostic in respect to natural botanical forms, would seem to be questions of fact, to be determined upon the evidence.

Of interest is Schorger's observation that the oils of non-typical western yellow pines (so-called cross-varieties) are not so constant as those of typical forms, though very closely related to it, being composed of terpenes. It is the writer's opinion that differences in oils of different forms of yellow pine by no means indicate intercrossing between this species and Jeffrey pine, but represent merely variations within the limits of the

ponderosa group. Jeffrey pine does not display such variation, the chemical composition of the oil being rather constant. This is in accordance with the morphological variations of yellow and Jeffrey pines, based on the writer's field experience. During the field work the question was often raised as to the possible intermixture of heptane and terpenes in the oleoresin of "non-typical" or intermediate pines (so-called hybrids) because of a yellow color or an apparently unusual, penetrating odor in the oleoresin. As this was a question of practical importance in the tapping of the trees, several samples of the "hybrid" oleoresins were examined without delay. The field test consisted of the distillation of the oleoresin with steam. The volatile oil was then redistilled with thermometer control, over direct flame. About 95% of the oil distilled below 100° C. (heptane), all of the remainder (a yellowish oil) having a boiling point above 200° C. No ingredients were found having boiling points corresponding to those of terpenes, or lying anywhere between the points named. In all (ten) cases considerable constancy was observed in the amount of heptane present. The morphological characters of these "hybrids" were found to be typical of Jeffreyi. In 1912, when the turpentine possibilities of the Pacific Coast were being studied, the same question arose as to intermediate forms between Jeffrey and yellow pines. At that time all "cross varieties" selected

were found to be turpentine producing trees and the conclusion was reached[25] that "unless a pine is typically Jeffrey it must be considered western yellow". In other words, all cross varieties have thus far been found within the limits of the ponderosa group.

So far as is known to the writer there are no direct statements in the special literature in regard to the possibility of natural hybridization between P. jeffreyi and P. ponderosa. The general opinion of local people is rather strongly in favor of the occurrence of intercrossing of the two. This notion is based mainly on the difficulties of field distinction between the two species. The question has not been scientifically studied thus far. Fortunately definite experiments in controlled crossing of these species are an early possibility. Observation during the tapping experiments of the Forest Service (in 1912 and 1927) gave uniformly negative results. In forest planting, also, the writer is informed, forest grown Jeffrey pine seed invariably results in typical Jeffrey seedlings, or seedlings at any rate in which divergence from typical form is undistinguishable. If hybridization occurred, there should be expected a proportion of clearly non-typical forms. It is worth while referring again to Baker and Smith's suggestion that "very definite knowledge is needed before one can accept the statement that such and such a tree is a hybrid under natural conditions".

In the foregoing discussion it is attempted to show (summarizing broadly):

1. That there are numerous morphological diagnostic characters between P. jeffreyi and P. ponderosa, respectively, which make it reasonably easy to distinguish specimens typical of either.

2. That in non-typical trees, which are numerous, variation may be so great in practically all the morphological characters as to overlap widely, and thus to obscure the relation.

3. That these non-typical forms are shown to be referrable mostly to P. ponderosa, by practically the only diagnostic character as between these species, which the work discussed has shown to be constant and stable, namely the chemical composition of the oleoresins.

4. That while the validity of chemical composition as a basis of species diagnosis is strenuously objected to by some botanists, it has also had some able defenders; but no one seems to have done conclusive investigative work upon it.

All but the fourth point concern facts, established by various investigators. The fourth is submitted to botanists as a subject promising considerable value for taxonomics in return for the labor of submitting it to statistical study as a matter of equally determinable fact, rather than to discard it on a priori grounds or those of analogy.

Acknowledgment is made to Director E. I. Kotok, and Mr. C. L. Hill, in charge of Forest Products research, of the California Forest Experiment Station, under whom the experimental work of the author on these species was conducted; also to Mr. Duncan Dunning and especially to Mr. Hill for criticism and assistance in the preparation of this paper.

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PLATE I

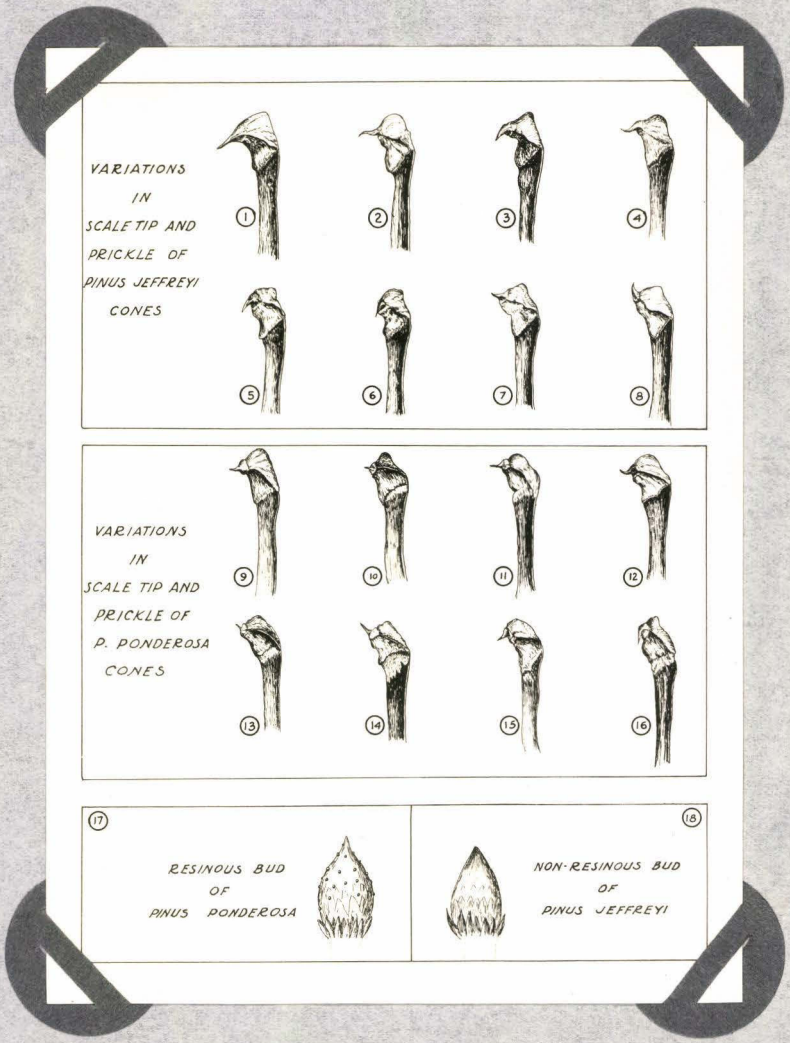
VARIATIONS IN SCALE TIP AND PRICKLE OF PINUS JEFFREYI CONES
1
2
3
4
5
6
7
8
VARIATIONS IN SCALE TIP AND PRICKLE OF P. PONDEROSA CONES
9
10
11
12
13
14
15
16
17
RESINOUS BUD OF PINUS PONDEROSA
18
NON-RESINOUS BUD OF PINUS JEFFREYI

PLATE II

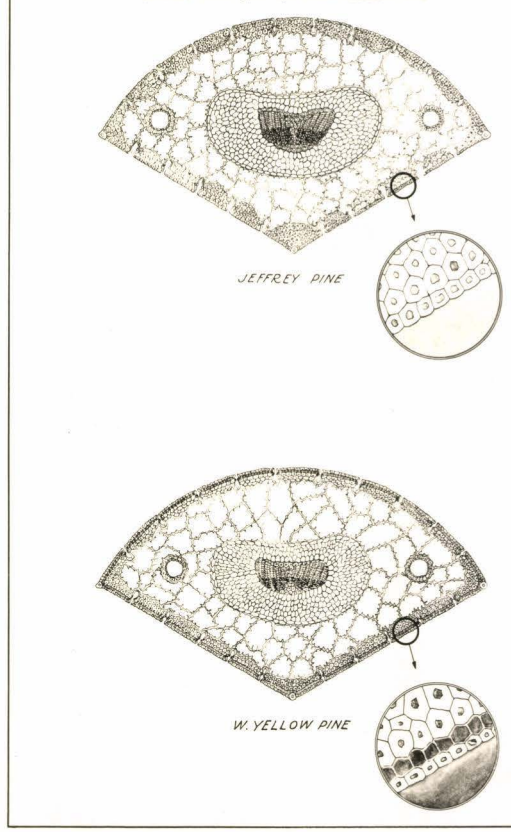
FIG.
INTERNAL STRUCTURE OF LEAVES OF JEFFREY PINE AND WESTERN YELLOW PINE
JEFFREY PINE
W. YELLOW PINE